Chapter 1

General introduction: interspecific interactions in a warming world

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Key-words: passerines, tits, flycatchers, climate change, competition, social information, phenology, timing

The evolution of seasonality

Most organisms have evolved annually recurring (circannual) rhythms (phenology) across different levels of biological organization that help them to survive and reproduce successfully (Perrins 1970; Verhulst and Nilsson 2008; Helm *et al.* 2013). Therefore, many animals are adapted to respond to environmental conditions that provide predictable timing cues, including day length and temperature (Bradshaw and Holzapfel 2007). Since breeding at the right time confers fitness advantages (Verhulst and Nilsson 2008), it is important to be aligned with seasonally changing conditions. For example, many passerines in temperate environments rely on a short peak in caterpillar abundance (Perrins 1991; Cholewa and Wesołowski 2011), the timing of which depends largely on temperature. Hence, the timing of passerines is thought to be evolved in part to respond to temperature (Visser *et al.* 2010). A more basic cue (one that is partly predictive of temperature in temperate environments) is photoperiod, a cue that triggers seasonal biological events including hibernation and migration (Dawson *et al.* 2001; Helm and Gwinner 2006; Helm *et al.* 2013), both of which are considered adaptations to cope with environmental harshness (and not with shortening photoperiod itself). During the breeding season, the seasonal environment imposes selection pressure on individuals reproducing at different day lengths. Therefore, over evolutionary time, it can be expected that one particular day length (photoperiod) in a certain population is correlated with the best mean fitness, ultimately causing stabilizing selection on breeding date (Bradshaw and Holzapfel 2007), resulting in timing adaptations that respond to photoperiod. Circannual programmes are at their basis considered to have evolved to respond to photoperiod (Gwinner 1967; Visser *et al.* 2010; Helm *et al.* 2013), and may be fine-tuned by other environmental variables, including year to year variation in temperature or food conditions.

Climate change and trophic mismatch

Over the period 1850–2012, global land and ocean surface temperatures have risen by 0.85 (±0.20) °C and are expected to continue rising over the next decades (IPCC 2013). Understanding the effect of climate change on ecological communities is important, as warming temperatures directionally alter ecological conditions. Among the best documented changes are geographical range shifts (Parmesan *et al.* 1999; Davis and Shaw 2001; Thomas *et al.* 2001), advances in spring phenology (Visser and Holleman 2001; Winkler *et al.* 2002; Parmesan and Yohe 2003; Thackeray *et al.* 2010, 2016), and trophic mismatch (Visser *et al.* 1998; Both and Visser 2001; Both 2010a). Trophic mismatch occurs in seasonally fluctuating systems, when resources peak at a different time than optimal for the trophic level that depends on these resources. This phenomenon was first demonstrated in a system with fish and plankton, where the recruitment of fish was higher when the synchrony with plankton supply was higher (Cushing 1969, 1990). Later, mismatch between oaks *Quercus robur*, winter moths *Operophtera brumata*, and

great tits *Parus major* was shown to occur as a result of climate warming (Visser *et al.* 1998; Visser and Holleman 2001), and a new field of inquiry was born. Since then, many studies have shown that phenological mismatch between trophic levels occurs (Edwards and Richardson 2004; Pearce-Higgins *et al.* 2005; Visser and Both 2005; Both *et al.* 2009; Thackeray *et al.* 2010; Saino *et al.* 2011) and has consequences for individual fitness (Durant *et al.* 2007; García-Navas and Sanz 2011; Reed *et al.* 2013b; Samplonius *et al.* 2016a) and in some cases even on population numbers (Both *et al.* 2006, 2010; but see Reed *et al.* 2013a). Logically, the question arose to what extent and by what processes animals and populations could keep up with a warming planet (Visser 2008).

Phenological advancement to climate change: adjust or adapt?

Animals or animal populations are broadly expected to adjust in two ways to climate change: within individual phenotypic plasticity or evolutionary changes. Phenotypic plasticity is the ability of organisms to produce different phenotypes with the same genetic background in response to environmental variation (Pigliucci 2005). Genetic adaptation occurs when selection for heritable genes favours certain timing schedules compared to others. Conceivably, late birds perform worse when their food peaks advance quickly, and genes for late timing would be selected against. A recent meta-analysis of long term studies on reproductive timing in birds revealed that almost every study that has considered avian phenological adjustment to climate change found evidence for phenotypic plasticity as the main mechanism underlying the apparent changes (Charmantier and Gienapp 2013). However, it was also stressed that evolutionary changes are seldom considered and are hard to prove from time series analyses. So far, only few studies have claimed a genetically underpinned evolutionary change in timing (Jonzén *et al.* 2006, disputed by Both 2007), and adjustment in arrival date (Van Buskirk *et al.* 2012).

Phenological components of interspecific interactions

Adjustment to climate warming has often been viewed from an among trophic level perspective, because this reproductive timing is thought to be regulated by the timing of shifting food conditions (Perrins 1970). However, reproductive decisions may also be governed by competition, the strength of which may be altered by climate change. Climate change may affect the timing of lower trophic levels more than higher ones, because mechanisms to regulate seasonal timing may differ among species groups, including temperature sensitivity, or the importance of other cues used to regulate timing like photoperiod (Thackeray *et al.* 2016). Alternatively, species groups may differ in the timing of their climate windows, for example because they have vastly different annual cycles (resident versus migrant), which may lead to differential changes if changes in temperature across these climate windows are asymmetrical (Thackeray *et al.* 2016). Such differential mechanisms to adjust to climate change are often studied among trophic

levels, but few studies consider differential responses to temperature within trophic levels. For example, it was shown that migratory flycatchers in Great Britain are less responsive to temperature changes than resident tits in the same system (Phillimore *et al.* 2016). Similarly, a meta-analysis showed that short distance migrants advance more than long distance migrants (Usui *et al.* 2017). If species differentially respond to climate change, then it is conceivable that interspecific synchrony within the same guild is affected, which may in turn have consequences for interspecific interactions within trophic levels. However, there is very little research on the effect of synchrony on consequences for species interactions, and whether it is present or not depends largely on whether and how species within the same guild compete over (different) resources.

Study system and first literature exploration

European great and blue tits *Cyanistes caeruleus* and pied *Ficedula hypoleuca* and collared flycatchers *F. albicollis* have become model systems to study adaptation to climate change, as they are nest box breeders with long-term data collected throughout their breeding ranges (Visser *et al.* 1998, 2003, 2004, 2011, 2015, Both and Visser 2001, 2005, Both *et al.* 2004, 2006, 2009; Visser and Both 2005; Visser 2008; Both 2010b; Goodenough *et al.* 2010; Bauer *et al.* 2010; Husby *et al.* 2011; Reed *et al.* 2013b; Samplonius *et al.* 2016a). Great and blue tits are European (mostly) resident species that spend the winter near their breeding location (although more northern population do migrate to some extent). Pied flycatchers are long distance migrants that winter in West-Africa (Ouwehand *et al.* 2016), whereas collared flycatchers spend the winter south of the equator (Briedis *et al.* 2016). The long distance migrant flycatchers have a later phenology than the resident tits with on average two weeks separating their mean laying dates in our study population in Drenthe (Box A). European tits and flycatchers are among a range of bird species facing relatively new pressures from anthropogenic climate change, because the phenology of their caterpillar food advances faster than they can keep up with (Visser *et al.* 1998; Both *et al.* 2009). All four species are common cavity nesters that depend on similar resources including nesting cavities and food (Török 1986), although relatively little is known about the similarity of their diets. Moreover, they all readily breed in nest boxes, for which there may be fierce competition (Slagsvold 1975). Furthermore, there is an increasing amount of evidence that this niche overlap leads to benefits for flycatchers by eavesdropping on the information provided by resident species (Forsman *et al.* 2002), coined heterospecific attraction (Mönkkönen *et al.* 1990).

Differential adjustment to climate change: a first exploration

To explore interspecific differences in laying date trends, we assembled published trends in laying dates of sympatric European tits and flycatchers (Winkel and Hudde 1997; Visser *et al.* 2003; Both *et al.* 2004, 2009; Goodenough *et al.* 2010; Bauer *et al.* 2010). In

most sympatric populations both tits and flycatchers have advanced laying dates (Figure 1.1). However, more information is required to answer questions regarding these interspecific differences. First, published trends are not standardized across years, making comparisons between trends problematic. This becomes evident when comparing trends from the same Dutch population in two different studies (Figure 1.1, grey text) with slightly different year intervals. Especially the difference in great tit trends is notable, raising the question of how sensitive such comparisons are to starting and ending year. Secondly, not all these studies correlated laying date trends with spring temperature, and if they did the period was not standardized between populations, ranging from "the 30-day mean temperature before mean laying date" (Visser *et al.* 2003; Both *et al.* 2004) to "mean entire spring temperature" (Bauer *et al.* 2010). Therefore, in order to explore interspecific differences in climate related phenological trends between tits and flycatchers across Europe, priority should be given to assembling long term data and standardizing them across years and temperature periods. Differences in phenological adjustment may affect interspecific synchrony and thereby interactions between tits and flycatchers, so first I will provide an overview of the type of interactions that may be affected by climate change in this study system.

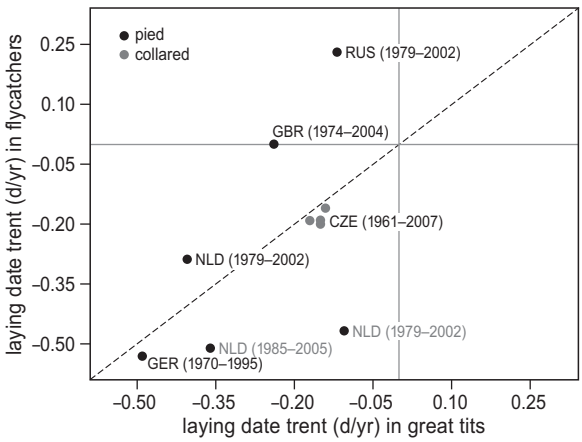

Figure 1.1 Published laying date trends of great tits and flycatchers breeding sympatrically in seven populations across Europe. Trends above the x = y line imply divergence of laying dates, whereas below the line they imply convergence. Populations with grey text are the same populations published in different studies with different years. Variable year intervals make population comparisons somewhat problematic.

Interactions between tits and flycatchers during the breeding season

Interference competition for nesting holes

"Campbell (*Bird Notes*, Vol. xxiii, p.227) has recorded a case of a dead Pied Flycatcher (*Muscicapa hypoleuca*) being found under a Great Tit's nest. The same author confirms my impression that Pied Flycatchers not infrequently usurp nesting sites tenanted by other species or build afresh on top of nests from which a brood has already flown."

(Mackenzie 1950)

When pied flycatchers arrive from their West-African wintering grounds to their temperate breeding grounds, the search for a nesting hole ensues. Male flycatchers arrive roughly a week earlier than females (Both *et al.* 2016), but more importantly tits will already have initiated nest building or egg laying. Therefore, nesting holes utilized by flycatchers in a previous year may have become occupied by a tit in the current year. Since tits already occupy many existing holes, flycatchers either have to find a new hole or try to evict a breeding tit, which they may attempt either by fiercely attacking tits outside of the nest box until they desert, or rapidly building a nest on top of the tit nest (Slagsvold 1975). However, taking over a tit nest is a risky endeavour, which may result in flycatcher mortality (Löhrl 1950; Mackenzie 1950; von Haartman 1956, 1957; Slagsvold 1975). Interestingly, flycatchers die in a tit nest box mostly during the egg laying phase of great tits (Merilä and Wiggins 1995). The explanation for this may be twofold. First, great tits spend more time away from the nest during egg laying, which increases the opportunity for flycatchers to take-over the nest, but also their risk to be caught off guard inside a tit nest. Second, male great tits spend more time in close proximity to their female partners during egg laying, guarding her during her fertile period (Björklund and Westman 1986). Therefore, it is conceivable that male tits are also most aggressive during this phase as they have to fend off potential rivals that might mate with their partner. Moreover, the ability of great tit males to defend from invading flycatchers appears to be correlated to social dominance, as measured by the broadness of their breast stripe (Winge and Järvi 1988).

Nesting holes are limiting population numbers in natural situations (Newton 1994). However, does this limitation also apply in nest box studies where the number of available nesting holes is artificially increased? Effects of the number of nest boxes on the number of breeding pied flycatchers have been amply recorded. In an entertaining quote, Von Haartman (1956) noted that "few ornithologists are probably wealthy enough to supply more nest-boxes in an area of 4 sq. km. than the Pied Flycatchers can use". Furthermore, in one of the first experiments in this study system in 1958, Campbell (1968) noticed that the pied flycatcher population size increased when he blocked entrance holes to keep tits from breeding until flycatchers arrived. Slagsvold (1978) used the opposite approach by blocking all empty nest boxes before flycatchers arrived, which dramatically reduced the number of breeding pied flycatchers in his nest boxes. Although these results appear to demonstrate that nest hole availability limits pied flycatcher

breeding densities, they have a limitation: the lack of a control group. It took another decade before the question whether tits and the number of nest sites limit breeding densities of flycatchers was finally resolved. Inspired by the first experimental demonstration that cavity roosting great tits limit the number of winter roosting blue tits (Dhondt and Eyckerman 1980), Gustafsson (Gustafsson 1988) upregulated nest box densities in three of his plots. The other half served as controls. The main result was that collared flycatcher numbers increased compared to his controls, proving that the number of available nesting holes limited collared flycatcher numbers. Moreover, in one plot he removed tits from nest boxes to show a dramatic increase in Collared Flycatcher occupation compared to controls, demonstrating that competition with great tits is one of the main processes limiting flycatcher numbers. In our own study population in Drenthe, it was found that pied flycatcher population numbers increased about fivefold after the initiation of the nest box study in 2007 (Both *et al.* 2017). The main conclusion is that even in semi-artificial situations like in nest box studies it was possible to demonstrate that nesting holes are limiting population numbers of cavity nesting birds. Therefore, in natural situations where fewer suitable holes are available, such competition must be even more intense. Nest box studies have greatly contributed to understanding the structuring role of interference competition in forest bird communities.

Exploitation competition for food

"As species of the same genus have usually, though by no means invariably, some similarities in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera."

(Darwin 1859)

It is generally accepted that competition is more severe within species than among species, as more similar individuals have more similar requirements, but interspecific competition can still have a meaningful effect on bird communities (Root 1967; Dhondt 2012). Within guilds there is more variation in foraging tendencies than within species, a concept first studied in detail in European titmice. In the forests of the English midlands, it was found that different species of titmice differ in their niche in terms of foraging height, and "preferred" tree species (Hartley 1953; Gibb 1954). Similarly, some studies noted more distinct foraging habits when species foraged together compared to when they foraged alone (Morse 1967; Hogstad 1978). Nevertheless, this observational evidence was criticized, because cause and effect could not be distinguished (Connell 1980). In order to establish the existence of interspecific competition in shaping the foraging niche, experimental removals had to provide conclusive evidence. Surprisingly, not only was it shown that experimental removal of dominant species resulted in expansion of the foraging niche of the subordinate species, but the removal of subordinate species also resulted in niche expansion of the dominant species (Alatalo and Gustafsson 1985; Alatalo and Moreno 1987). Such results show that interspecific competition is reciprocal

and that even dominant species incur costs of competition from subordinate species. Although amply studied separately (Royama 1970; Sanz 1998; Cholewa and Wesołowski 2011), only one comparative study was found on foraging in European tits and flycatchers, which showed that the niche (or more precisely nestling diet) overlap between tits and collared flycatchers in Hungary was 33% (Török 1986), although this was only analyzed at the Order level. However, no experimental studies were found, showing a general lack of information about the effects of competition between these resident and migratory birds on their foraging tendencies.

To prove that interspecific competition takes place, diversifying foraging patterns should translate into fitness consequences (Dhondt 2012). Fitness consequences of interspecific competition are generally viewed from a density dependent perspective. However, intraspecific density dependence of clutch size was found in half of the studies on tits, but in zero of the studies on flycatchers (Both 2000). This pattern was hypothesized to be attributable to the unpredictability of final breeding densities for the migratory flycatchers, but this did not turn out to be true. An alternative hypothesis was that flycatchers were more limited by indivisible resources (nesting holes) than by divisible resources (food) in nature, and that therefore no intraspecific density dependent patterns were found there (Both and Visser 2003). Interestingly, a third hypothesis - that flycatchers are more subjected to interspecific than intraspecific density dependence – was not considered in these studies. However, such a hypothesis is supported by both observational and experimental studies. In one study, 19 years of data showed that high great tit densities negatively impacted collared flycatcher clutch size and fledgling success, and high collared flycatcher densities negatively affected both blue and great tit hatching success and fledging success in great tits (Sasvári *et al.* 1987). This effect was not found in another study, possibly due to their relatively low tit densities and very high flycatcher densities compared to the other study, which potentially increased the effect of intraspecific competition (Török and Tóth 1988). Gustafsson (1987) proved that experimental density reductions of great tits had a positive effect on collared flycatcher fecundity, fledgling weight, and recruitment. A more recent study demonstrated negative effects of high experimental tit densities on collared flycatcher *Ficedula albicollis* clutch size, fledgling mass, and number of fledglings (Forsman *et al.* 2008). In yet another study, negative effects of pied flycatcher densities on great tit chick growth were found (Forsman *et al.* 2007). In short, there is both observational and experimental evidence that flycatchers and tits negatively affect each other's fitness through exploitation competition, although most of this evidence was found in collared flycatchers. Moreover, there is no evidence whether species may affect each other's optimal timing response to climate change.

Positive interactions between resident and migrant passerines

Over the past decades evidence has emerged that competing species not only negatively affect each other, but they may also provide information for settlement and reproductive decisions, a process coined heterospecific attraction (Mönkkönen *et al.* 1990). The predictions for such attraction oppose that of competition, as it is expected that cue users should be more attracted to higher rather than lower numbers of information providers,

which may signal high habitat quality. Landscape scale manipulations of resident tit densities have so far mostly been done in Scandinavian studies, and have tentatively confirmed that heterospecific attraction plays a role in settlement decisions, but the effects have varied across studies and species groups. Positive associations between manipulated tit density and the numbers of different bird species were found, including willow warblers *Phylloscopus trochilus* (Mönkkönen *et al.* 1990), increased chaffinches *Fringilla coelebs* (Mönkkönen *et al.* 1990; Thomson *et al.* 2003). For unclear reasons, another study excluded those two species from the analysis and found a positive effect on the rest of the "migrant foliage gleaning guild" (Forsman *et al.* 2009). Yet another study found an effect of tit density only on redwing *Turdus iliacus* (but with a very low sample size: 8 vs 2 breeding pairs) numbers (Forsman *et al.* 1998). So far, the results of landscape scale manipulations of tit densities have pointed toward effects on settlement patterns of migratory birds, but the results remain somewhat ambiguous.

Apart from broader landscape scale effects when choosing a suitable breeding habitat, animals may use more local information to optimize their settlement and reproductive decisions. Settling pied flycatchers regularly visit tit nest boxes (Forsman and Thomson 2008), a behaviour that is also common in a conspecific setting (Ottosson *et al.* 2001). The outstanding hypothesis is that flycatchers visit other nest boxes to gather inadvertent social information about habitat quality (Danchin *et al.* 2004). Moreover, tits are often further advanced in their phenology, so their information may be more useful to late arriving flycatchers than that of early arriving conspecifics. When settling flycatchers were made to choose between two types of geometric symbols on empty nest boxes, later arriving inexperienced flycatchers were more likely to copy the symbol choice that was associated with tit occupation, whereas experienced flycatchers were indifferent, possibly relying more on personal information (Seppänen and Forsman 2007). Moreover, the pied flycatcher's decision to copy or reject a great tit symbol was correlated with the number of eggs or offspring that was present in the tit nest at the time the choice was made (Forsman and Seppänen 2011; Seppänen *et al.* 2011). This effect in turn appeared to disappear when information was hidden due to tits covering their eggs (Loukola *et al.* 2013), a behaviour which was overexpressed when songs of flycatchers were played outside the tit nest box (Loukola *et al.* 2014a). To summarize, many studies both at the landscape scale and at the nest site scale have found that birds use social information in their breeding site selection, which is contrary to the classic idea that only negative effects induced by competition regulate community composition.

A brief overview of studies on interactions between tits and flycatchers can be found in table 1.1.

Emerging knowledge gaps

From studying the literature on adjustment to climate change and interspecific competition between tits and flycatchers, it is clear that few studies consider whether tits and flycatchers may adjust at different rates to climate change and how this may affect inter-

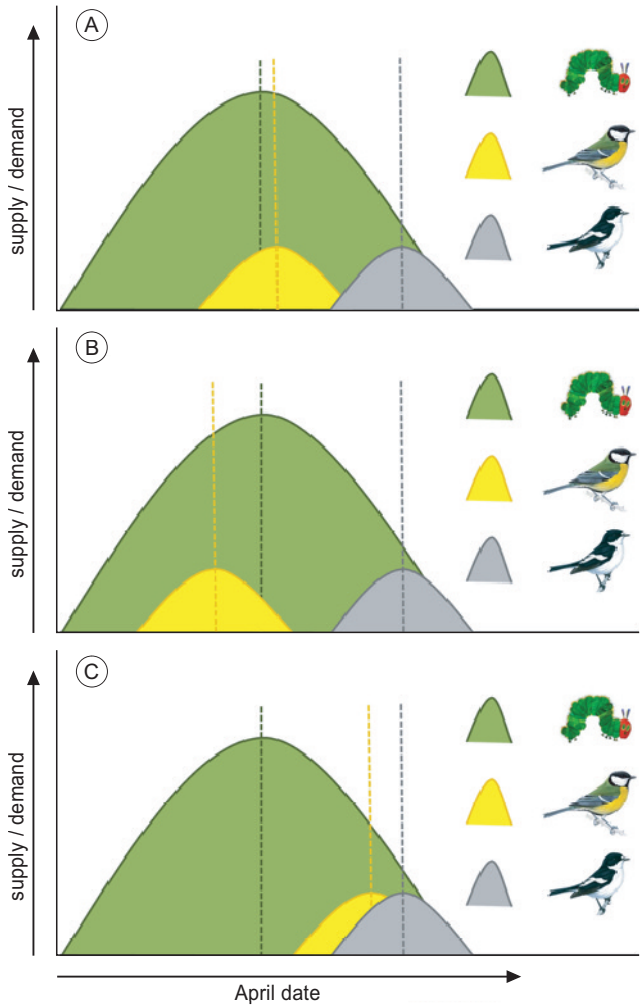

Figure 1.2 Schematic overview of the expected outcome of experimental manipulations of tit timing. In some forest patches, tits were advanced (B) relative to the original distribution (A), whereas in other forest patches they were delayed (C), creating different degrees of overlap with breeding pied flycatchers.

specific competition. Could species that depend on similar resources indeed change each other's optimal response through interspecific competition or are the responses mostly driven by underlying trophic levels (food) or even higher trophic levels (predators)? More generally, competition and information use are not generally viewed from a timing perspective, but mostly from a density dependent perspective. Competition may not only intensify because the caterpillar peak shifts faster than avian phenologies (potentially leading to food shortages), but also because differential rates of adjustment may cause a higher degree of synchrony between competing species (although synchrony could also

be reduced). There is evidence that synchrony between tits and flycatchers causes a higher degree of flycatcher mortality, but this was only studied in one Finnish population so far (Ahola *et al.* 2007). Moreover, information use may have temporal components, because areas in which tits breed earlier could be preferred if flycatchers are to avoid temporal components of competition. Alternatively, a high habitat quality could cause tits to breed early (Svensson and Nilsson 1995; Lambrechts *et al.* 2004), and therefore tit phenology may be an indicator of habitat quality for settling flycatchers.

Outline of the thesis

The aim of the current thesis is to understand the decisions and pressures pied flycatchers face under climate change, with a focus on interactions with the great tit. In box A, I present an anecdote to provide some more context as to how I came to the questions studied in this thesis. Counterintuitively, after this anecdote in chapter 2, I present an intertrophic perspective on the effect of timing and nestling age on the nestling diet of the pied flycatcher, but this also provides an important basis for the rest of the work, because it gives an overview of the foraging ecology of pied flycatchers in our study system, which may also be affected by interspecific competition. Moreover, it provides a perspective on the effects that underlying trophic levels have on the response of flycatchers.

To study differential effects of temperature on resident and migrant cavity nesters, in chapter 3, I provide a collaborative analysis of long-term data from 10 populations of tits and flycatchers across Europe. Here, I also study whether phenologies of these species groups have generally converged or diverged and speculate what implications this could have for synchrony, competition, and information use. This information use part of the question is further elaborated in chapter 4, in which I performed an experimental study where the phenologies of great tits were advanced and delayed at the subplot level (Figure 1.2) and flycatcher settlement patterns were monitored. To further investigate the information use question, we also performed a study in which we used geometric symbols (chapter 5) to study whether conspecific or heterospecific information is preferred by flycatchers. Subsequently, in chapter 6 I analyze how synchrony with great tits in combination with great tit density affects pied flycatcher mortality patterns during the settlement phase (interference competition). Last, I study whether our experimental manipulations (chapter 4) affected great tit and pied flycatcher nestling diets and offspring condition. I will end this thesis with a general discussion on the results in chapter 8, where I will emphasize the importance of synchrony in modulating species interactions, especially during the settlement phase of cavity nesting passerines in our population. Table 1.2 gives a concise overview of which data was collected when and in which chapters it was used.

Table 1.1 Studies about interactions between Paridae and Ficedula spp. Descriptive studies are at the top half and experimental ones at the bottom half of the table. Types of effects: Interference (I), Exploitation (E), Asymmetrical (A), Facilitation (F), Year effect (Y).

Descriptive studies	Main findings	Type of interaction	Reference
Tit related flycatcher deaths	More flycatchers probably killed by great tits than by predators	I	(von Haartman) 1957
Eight hole nesters are analyzed and assigned to being either a "host" or an "aggressor"	11 out of 29 mixed clutches successful, always raised by the host; 12 cases of F. hypoleuca evicting *P. major* during egg laying period, only one the other way around	I	(Busse and Gotzman 1962)
Nest box competition	Three females killed in nest boxes; In high flycatcher density years, nest takeovers by *F. hypoleuca* were observed more regularly (5 times in one year than in lower density years)	I	(Tompa 1967)
General description of territory mapping, spatial distribution of 24 insectivores	*F. hypoleuca* aggressively defend territories, but may have overlap with others; Both inter- and intraspecific fighting occurred along territorial boundaries. Species may be separated horizontally, vertically or by the types of food taken	I / E	(Edington and Edington 1972)
General description of aspects of interspecific competition *P. major* and *F. hypoleuca*	*F. hypoleuca* may take over *P. major* nests, *F. hypoleuca* takes a greater variety of prey than *P. major* and has a different hunting technique, but there is dietary overlap; Negative correlation *P. major* density and *F. hypoleuca* clutch size in Von Haartman's data, but not in forest of Dean, *F. hypoleuca* success higher in late food peak years; High *P. major* density year 1 negatively affected *F. hypoleuca* density year 2 in Finland, but positively in England	I / E	(Slagsvold 1975)
Food segregation and overlap *P. major*, *P. caeruleus*, and *F. albicollis*, diet composition measured by neck collars 1978–1982	Niche breadth F. albicollis larger than the two tit species with regard to food composition, but not with regard to prey size; Niche overlap prey type + prey size: *P. major* - *P. caeruleus* 0.54 + 0.49; *P. major* - *F. albicollis* 0.33 + 0.35; *P. caeruleus* - *F. albicollis* 0.45 + 0.56	E	(Török 1986)
Intra- and interspecific density dependence of reproduction were studied in *P. major*, *P. caeruleus*, and *F. albicollis*; 19 years of data	High blue tit density reduced great tit clutch size, but not the other way around; High densities of *F. albicollis* increased hatching failure in great and blue tits, and decreased fledging success in great tits; Years with high densities of *P. major* had significantly reduced *F. albicollis* clutch size and fledging success	E	(Sasvári *et al.* 1987)
Observe how *P. major* nest defense success against *F. hypoleuca* is related to Parental Investment or Fighting Ability	Great tits with larger breast stripes were better able to defend against pied flycatchers, supporting Fighting Ability hypothesis; No support for the Parental Investment hypothesis which postulates that parents should become more successful at defending their nest depending on their breeding stage	I	(Winge and Järvi 1988)
Description of 23 *F. albicollis* casualties in *P. major* nest boxes in 1993	4.3% of *F. albicollis* population killed by *P. major* (varying between 0 and 17%), 18 out of 23 were male, no effect of age class on casualty probability; Most deaths among early arriving *F. albicollis*, during egg laying phase of *P. major*; *F. albicollis* casualty rate significantly correlated with *P. major* density	I	(Merilä and Wiggins 1995)
53 *F. hypoleuca* casualties in *P. major* nests; 53 years of data	Casualty rate negatively correlated with laying date interval between the species; Casualty rate positively correlated with *P. major* and *F. hypoleuca* density; Laying date interval significantly correlated with the difference in species specific temperature response in laying date	I	(Ahola *et al.* 2007)

Table 1.1 Continued.

Descriptive studies	Main findings	Type of interaction	Reference
attach cameras to 80 blue and great tit nest boxes, record flycatcher visits	10 flycatcher (both species) visits in 129 hours of recording; No effect of feeding rate, year, or nestling age on visiting probability	F	(Forsman and Thomson 2008)
Block nestboxes to prevent tit breeding	local tit population declined; *F. hypoleuca* population increased	I	(Campbell 1968)
Provide nest-boxes	Large increase pied flycatchers; No effect on other breeding bird numbers	No	(Enemar and Sjöstrand 1972)
Block empty nestboxes to encourage *F. hypoleuca* takeover	2 out of 40 nests taken over by *F hypoleuca*; one killed; breeding density reduced; 4 takeover attempts, where female *F. hypoleuca* carried nest material in *P. major* nest	I	(Slagsvold 1978)
Reduce *P. major* density in both high and low density plots by 90%	*F. albicollis* density increases; *F. albicollis* clutch size, nestling mass, and fledging success higher in low *P. major* densities	I / E	(Gustafsson 1987)
Manipulate nest-box density and number of tits breeding, provide small and larger nest boxes	Reduction tit numbers; increase in *F. albicollis* numbers in high nest box densities; F. albicollis adults breeding in smaller boxes have reduced breeding success and smaller tarsi	I	(Gustafsson 1988)
Manipulate nest box density, a four year study	Tit density varied 0.8-1.8 pairs/ha; *F. albicollis* density 2.1–9.1 pairs/ha. No effect of tit density on *F. albicollis* reproductive traits (probably because of their low breeding density); *F. albicollis* hatching, fledging, and breeding success, and fledgling tarsus length negatively correlated with intraspecific density	E	(Török and Tóth 1988)
Add / remove resident Parus spp on 6 different islands	Increase chaffinch (18 vs 22), willow warbler (35 vs 39), and other migrants (42 vs 53) on tit enriched islands; no niche shifts	F	(Mönkkönen *et al.* 1990)
Increase / decrease resident cavity nesters *Parus atricapillus*, *Sitta canadensis*, *Sitta carolinensis*	High first factor loadings of the "log transformed arboreal insectivore migrant densities" in high resident density year; No difference in migrant abundance, no difference in species richness	F? / (Y)	(Mönkkönen and Helle 1997)
Increase / decrease resident *Parus* spp densities	No effect on migrant densities; Increase redwing density (8 vs 2)	F? / No	(Forsman *et al.* 1998)
Reduce (in 3 plots) / increase *Parus* spp density (in 6 plots), after which 50 *F hypoleuca* settled	No effect on clutch size, nestling survival to day 13, tarsus; Marginally earlier settlement in tit enriched areas, positive effect of added tits on fledgling body mass and wing length	F	(Forsman *et al.* 2002)
Increase/decrease resident tit densities	More chaffinches in high tit densities; No effect on densities other birds	F? / (Y)	(Thomson *et al.* 2003)
Reduce (in 3 plots) / increase tit density (in 6 plots)	Seasonal decline in brood size and offspring size *F. hypoleuca* in "tit removal" plots, but not in "tit enriched" plots; More inexperienced females in "tit removal" plots	F / E	(Seppänen *et al.* 2005)
Attach same geometric symbol on all tit boxes in area, divide remaining half of nestboxes 50/50 with same/different symbols	Late (inexperienced) flycatchers copied heterospecific nest box choice; No effect of early flycatchers on nest box choice	F	(Seppänen and Forsman 2007)

Table 1.1 Continued.

Descriptive studies	Main findings	Type of interaction	Reference
Forced great tits and pied flycatchers to breed in close proximity vs far away from each other 2003–2005	No effect on *F. hypoleuca* reproduction; In absence of flycatcher, *P. major* chicks were 9,6% heavier in 2003 + 2005 (no effect 2004). 12,4% longer wings in 2003 (no effect 2004 + 2005), and 2% longer tarsus in all years	A	(Forsman *et al.* 2007)
Create density gradient of *P. major* between plots	*F. albicollis* settle earliest at intermediate tit densities; *F. albicollis* have lower clutch size, fewer nestlings, smaller nestling tarsus, and lower fledgling body mass at high tit densities; opposite pattern for low tit densities	E / F	(Forsman *et al.* 2008)
Create density gradient of *P. major* between plots	Migrants (species number and density) increase linearly with tit density	F	(Forsman *et al.* 2009)
Attach same geometric symbol on *P. major* boxes, place empty box with opposite symbol immediately adjacent. Place two empty boxes 25 m away with same symbols, monitor *F. hypoleuca* choice	*F. hypoleuca* reject tit "choice" if fitness correlate is low; *F. hypoleuca* copy tit "choice" if fitness correlate is high	F	(Seppänen *et al.* 2011)
Attach same geometric symbol on simulated (fake) *P. major* nests with either 4 eggs or 13 eggs, place empty box with opposite symbol immediately adjacent. Place two empty boxes 25 m away with same symbols, monitor *F. hypoleuca* choice	Most birds nest on top of simulated nest (40 out of 58), building 40% smaller nests; Of the (n = 12) low simulated *P. major* fitness nests, 10 *F. hypoleuca* rejected, 2 copied	F	(Forsman and Seppänen 2011)
Attach same geometric symbol on simulated (fake) *P. major* nests with either 4 eggs or 13 eggs, place at least 1 empty box next to it, monitor *F. hypoleuca* investment decision	Young females lay fewer eggs with lower clutch mass; High simulated *P. major* fitness caused *F. hypoleuca* females to lay 6,9% more eggs that were 4.5% heavier in 2009 (but not in 2010), and a 9.3% heavier clutch	F	(Forsman *et al.* 2012)
Attach same geometric symbol on *P. major* boxes, place empty box with opposite symbol immediately adjacent. Place two empty boxes 25 m away with same symbols, manipulate clutch size of *P. major* (5 or 13), monitor *F. hypoleuca* choice	When information is available (no egg covering), *F. hypoleuca* copies *P. major* choice, but rejects it when information is unavailable (eggs covered); Young females more responsive to *P. major* manipulation	F	(Loukola *et al.* 2013)
Playbacks of pied flycatcher and redwing songs outside of great tit nest boxes, monitor egg covering propensity of great tits	Tits cover eggs more when a flycatcher song is playing outside its nest box	F / I	(Loukola *et al.* 2014a)

Table 1.2 Timeline of the thesis. An overview of data collected, experiments executed, and data analyzed, in which chapter this can be found, and in which years it was collected.

Year	Experiments / data	Data analyzed	Chapter
2013	Delaying flycatchers	Diet and offspring condition	2
2014 + 2015	Advancing and delaying tits	Flycatcher settlement, prey choice, and offspring condition; tit prey choice and offspring condition	4+7
2015 + 2016	Compiling long term data	Reproductive timing	3
2014 + 2016	Symbol experiments	Nest box choice	5
2007 – 2016	Monitor flycatcher victims	Flycatcher mortality	6

Box A

A case of a three species mixed brood after two interspecific nest takeovers

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Ardea (2016) **102**: 105–107

Key-words: interspecific interference competition, mixed broods, passerines, phenology

ABSTRACT

Mixed interspecific broods in hole nesting passerines occasionally occur as a by-product of competitive interactions for nest sites. Here, we report a rare case where such interactions led to a three species brood of pied flycatcher *Ficedula hypoleuca*, blue tit *Cyanistes caeruleus* and great tit *Parus major* nestlings that was successfully raised by a great tit pair. This occurred in an environment of relatively high temporal overlap in interspecific breeding timing.

During the breeding season, insectivorous hole nesting passerines compete for nest sites (Minot and Perrins 1986). Two species mixed broods resulting from these interactions have been reported occasionally (Mackenzie 1950; Arn 1955; Campbell 1968; Merilä 1994; Petrassi *et al.* 1998; Dolenec 2002; Borgström 2005; Suzuki and Tsuchiya 2010). Here we describe the special case of a three species mixed brood, where one nest box was sequentially occupied by a pied flycatcher, a blue tit, and a great tit, all of which laid eggs. The eggs were incubated by the final, great tit, female. Subsequently, six great tits, one blue tit, and two pied flycatcher chicks were raised to fledging. As far as we know the raising of three species in one nest has not been reported before.

The pied flycatcher is a migratory palaearctic passerine that winters in West Africa and breeds in Russia and temperate Europe (Cramp and Perrins 1993). On arrival at their breeding grounds, pied flycatchers have little time to decide on their breeding site. Therefore, part of flycatchers' habitat selection strategy is to use cues of resident species with considerable niche overlap like blue and great tits (Mönkkönen *et al.* 1990, 1999). Pied flycatchers not only utilize information of residents for their own breeding decisions (Seppänen and Forsman 2007; Forsman and Thomson 2008), but they are also notorious for taking over nests from tits, sometimes with deadly consequences for the flycatchers (Tompa 1967; Slagsvold 1975; Merilä and Wiggins 1995 in collared flycatchers *Ficedula albicollis*; Ahola *et al.* 2007).

The spring of 2013 was unusually cold: data from The Bilt (NL) meteorological station show it was the 5th coldest pre-breeding period (March 15 – April 14) since the start of measurements in 1901. This cold period resulted in delayed nest building by resident blue and great Tits. Laying date in all species was the latest since the start of the study in 2007 of our study areas Dwingelderveld (52°49'04"N 6°26'21"E, 400 nest boxes), Drents-Friese Wold (52°54'43"N 6°19'16"E, 550 nest boxes) and Boswachterij Ruinen (52°43'34"N 6°23'56"E, 100 nest boxes) National parks. Interestingly, pied flycatcher laying date was much less delayed (3.15 d later compared to 2007–2012) by the cold weather than in the tits (12.81 d later compared to 2007–2012). This resulted in the shortest laying date interval between tits (blue and great tits pooled) and flycatchers within this study (2013: interval 5.9 d, mean interval 2007-2012: 15.6 d, Figure A.1).

In concert with this late phenology, a highly peaked flycatcher arrival resulted in increased competition for nest boxes, especially in one of the oak dominated study sites (52°49'08"N 6°23'11"E, 50 nest boxes) with high densities of great and blue tits. This competition continued well into the egg laying phase, and takeovers not only went from flycatchers to tits, but also the other way around. Of 45 nests in this area, nine were takeovers, four of which went from pied flycatcher to blue tit, three from great tit to pied flycatcher, one from pied flycatcher to great tit, and one from blue tit to great tit. Of these takeovers however, only one resulted in a mixed brood.

On April 21, a pied flycatcher male had arrived at an unoccupied nest box in the aforementioned oak dominated study area and started singing. A female initiated nest building on April 24, after which the nest was completed on April 29, and the first egg appeared on May 7. However, during a routine nest box check on the May 9, we found a blue tit nest made of moss and feathers with two flycatcher eggs and one blue tit egg.

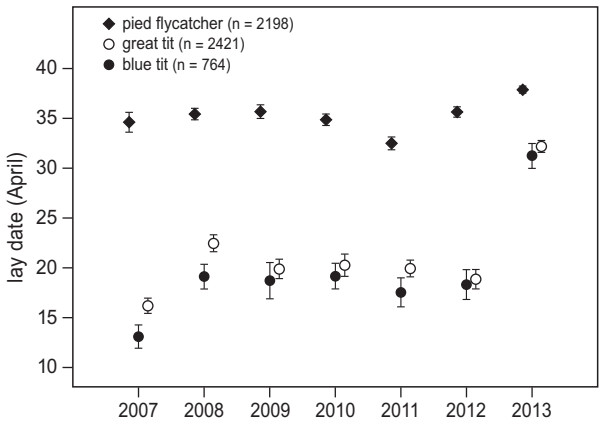

Figure A.1 Mean first brood laying dates and confidence intervals of three common hole nesting passerines in the populations Dwingelderveld (400 nest boxes), Drents-Friese Wold (550 nest boxes), and Boswachterij Ruinen (100 nest boxes) National parks. Note the large laying date shift (12.81 d) in tit species between 2013 and 2007–2012, compared to the smaller shift (3.15 d) of pied flycatchers.

One day later (May 10), we found two more eggs apparently laid at the same day, one of a great tit and the other of a blue tit (Figure A.2, left), but with no change to the nest material. The clutch was completed on May 16 now containing two pied flycatcher eggs, two blue tit eggs and seven great tit eggs. These were incubated by a female great tit and all eggs except one (great tit) hatched between the May 28–30. In the course of the following three weeks, one blue tit chick died, but the remaining nine chicks (Figure A.2, right) had fledged on the June 17.

The great tits did not seem to differentiate between chick types in the nest, because the two flycatcher young appeared to be fed normally, although one was underweight on day 12 (9.5 and 13.5 g; average of day 12 pied flycatcher chicks in 2013 was 13.87 g). Indiscriminant feeding was also observed in an interspecific cross-fostering experiment (Turtumoygard and Slagsvold 2010). As far as we know, the great tits were the only parents feeding the chicks, as they were the only ones alarming on frequent nest visits. Given that investing in offspring that are not your own is costly, why did the great tits not discriminate between their own and foreign young? It can be argued that the behaviour of covering up competitor eggs with nest material is usually sufficient to avoid their hatching, and selection on kin recognition in the nest may be weak, as mixed broods are rare. Moreover, even if interspecific eggs hatch, the young rarely fledge: in a previous study of mixed broods with pied flycatchers and great and blue tits, fledging success of interspecifically cross-fostered flycatcher young was three times lower than that of young in control broods (Slagsvold 2004).

Pied flycatchers are typically viewed as the "parasite" in nest takeovers, whereby the tits aggressively respond to intrusions (Slagsvold 1975; Merilä and Wiggins 1995; Ahola *et al.* 2007). However, this case shows that blue tits and great tits are also capable of taking over nesting sites. We hypothesize that the propensity to take over nests is not

merely a behavioural trait of flycatchers, but may be a more common phenomenon among hole nesting passerines. The explanation for rarely observing it in tits is that their breeding timing usually precedes that of flycatchers such that it rarely leads to interference competition for nest sites. We suggest that overlap in reproductive timing may increase interspecific competition between cavity nesting passerines.

Figure A.2 Left panel: two pied flycatcher eggs (left), two blue tit eggs (middle), and a great tit egg (right) after the second takeover. Right panel: a blue tit, two pied flycatcher, and six great tit chicks three days before fledging.

Part 1

An intertrophic perspective on asynchrony, prey choice and offspring condition